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The vegetation of Connecticut

VI. The plant associations of eroding areas along the seacoast*

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(WITH SIX TEXT FIGURES)

CONTENTS

I. INTRODUCTION

This paper, with another which will appear shortly, concludes a series of articles in which the vegetation of Connecticut has been considered primarily from the standpoint of physiographic ecology.† Since the appearance of the fifth installment of the

* Contribution from the Osborn Botanical Laboratory.

† For citation of earlier papers, see list of literature at end of the present paper.

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series, the writer has published a scheme for the classification of plant associations (Nichols, '17), which differs in certain important details from that heretofore followed, although based on the same fundamental principles. For the sake of uniformity with previous numbers of the series, however, this classification will be largely neglected in the present paper. It may be of interest to note that a revised and amplified account of the vegetation of Connecticut, to be published as a bulletin by the Connecticut State Geological and Natural History Survey, is in course of preparation.

It is a familiar observation to all who visit the seacoast that the vegetation here presents many unique types of plant association. The seaweed associations of rocky shores, the associations of salt and brackish marshes and of sandy beaches and dunes—these and other distinctively seaside associations and groups of associations form the subject of this paper and of the one which follows.

At the outset, brief attention may be called to a number of important papers relating primarily to the ecology of seaside vegetation along the northern Atlantic coast, and especially to one by Kemp ('62) on "the shore zones and limits of marine plants on the north eastern coast of the United States." This remarkably clear and interesting discussion, based primarily on the study of the seaweed associations in the Casco Bay region, Maine, probably represents the first published account of a distinctly ecological nature dealing with the marine vegetation of this country, yet it seems to have escaped the notice of all the more recent writers on this subject and has but lately been brought to the writer's attention by Mr. F. S. Collins.* Among other and

* In introducing his studies, Kemp remarks: "I was aware that all the Hand Books on the Algae had noted the special localities of each species, . . . but I was not aware that in any of the books, shore lines and limits of plant growth had been made the subject of special treatment. This subject may be regarded as a minor branch of the important enquiry as to the geographical distribution of plants." Kemp divides the "tidal shore" into "six distinct zones," as follows: (1) the drift or beach zone, (2) the *Ulva* zone, (3) the *Fucus* zone, (4) the *Laminaria* zone, (5) the *Chondrus* zone, (6) the deep sea zone. The vegetation of these zones he describes in graphic detail, both from a floristic and from an ecological point of view, and in this connection ventures many suggestive observations, of which the following may serve as an illustration. Commenting on the predominance of *Ulva* in the upper portions of the intertidal region, he remarks: "A reason for this may be that the bright green color

more familiar works, Shaler's classic papers on the beaches and tidal marshes of the Atlantic coast ('85, '95, etc.), while written from the standpoint of the geologist, contain much that is of ecological interest. Kearney ('00, '01, '04) has described the seaside associations along parts of the North Carolina and Virginia shores, and has discussed the ecological relations of beach and dune plants. Shreve and Chrysler ('10) have treated the seaside associations of Maryland, Miss Snow ('02, '13) those of the Delaware coast, and Harshberger ('00, '02, '09, '11, '16, '19) those of the New Jersey coast. Transeau ('13) has described the seaside vegetation in the vicinity of Cold Spring Harbor, Long Island, and Johnson and York ('15) have made an extended study of the relation of plants to tide levels in this locality. For Massachusetts, B. M. Davis ('13) has written on the algal vegetation in the vicinity of Woods Hole, and Townsend ('13) on the sand dunes and salt marshes of the Ipswich region. Ganong ('03, '06) has described the salt and diked marshes along the Bay of Fundy and sandy beaches in northern New Brunswick, Transeau ('09) the seaside vegetation of southern Nova Scotia, and Nichols ('18) the coastal associations of Cape Breton Island, in northern Nova Scotia. In addition to these papers, the works of Penhallow ('07), Bartlett ('09, '11), C. A. Davis ('10), and D. W. Johnson ('13), while concerned primarily with botanical evidences of coastal subsidence, contain numerous observations of general or special ecological interest; and Olsson-Seffer's articles ('10) on the sand formations and sand strand floras of marine coasts, although not dealing specifically with our coast, are also worthy of note, if for no other reason than the extensive bibliographies which they contain. Complete citations for these and for other papers which are referred to in this article or in the one which follows are given in the list of literature at the end of the present paper.

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which distinguishes most of the species requires a larger amount of sunlight for its production than the olive, and red-colored plants require which inhabit lower zones and deeper water. The color of these plants of the order *Ulvaceae* which travel into deep water, is for the most part of a darker hue than those which grow in shallow places."

II. HABITAT FACTORS ALONG THE SEACOAST

The character of plant associations along the seacoast, both above and below high tide level, shows the influence of the sea in various ways and to various degrees. Some of the ways in which this influence is expressed are summed up in the following paragraphs.

A. INFLUENCES ASSOCIATED WITH SUBMERGENCE IN SEA WATER

Salinity of sea water.—This very naturally holds first rank among the factors responsible for the peculiarities of vegetation which is within actual reach of the salt water. It results primarily in the exclusion of many plants and plant associations which are present in similar situations along the shores of large bodies of fresh water, such as the Great Lakes, and in the presence of many others, notably the marine algae, which are not represented elsewhere.

The water of the open ocean in the North Atlantic contains about 3.3 per cent of salt. Along practically its entire length the Connecticut coast faces on Long Island Sound, and the salinity of the Sound water is considerably lower than that of the open ocean.* This difference in salinity is to be expected, since the Sound is partially shut off from the ocean by Long Island and has several large rivers emptying into it. The difference is of importance, because it is doubtless correlated with the absence or scarcity in many parts of the Sound of seaweeds which are abundant in similar situations along the open ocean. All intergradations are to be found along the coast and in the adjoining waters between areas in which the water is strongly saline and areas in which it is fresh, and these variations in salinity are accompanied by corresponding variations in vegetation.

The tides.—Marine algae which grow above low tide mark must be adapted to very different environmental conditions from those that grow at lower levels. For a longer or shorter period each

* According to Graves ('08) the salinity of the water in the open Sound near New Haven is about 2.8 per cent. This figure probably represents a fair average for the entire area, but of course there is considerable difference between the salt-content of the water westward from New Haven, toward the head of the Sound, and eastward, toward its mouth.

day they are exposed to the air and therefore must be able to endure, in varying degree, desiccation, exposure to rain water, and intense illumination, not to mention freezing temperatures in winter. Similarly, halophytic seed plants which grow in areas that are permanently or intermittently submerged must be able to accommodate themselves, for longer or shorter periods, to poor aeration and weak illumination. It is the varying degree to which seaweeds and seed plants are adapted to these diverse environmental conditions that in large part is responsible for the zonal arrangement of plant associations in relation to tide levels (FIG. 5), which constitutes one of the most striking features of seaside vegetation.

The range of the tides along the Connecticut coast, *i.e.*, the difference between high and low tide levels, varies greatly in different localities. The average daily range at Greenwich, toward the western extremity of the Connecticut shore line and toward the head of the Sound, is nearly three times that at New London, toward the eastern end of the shore line and just outside the entrance to the Sound. Proceeding from east to west along the Connecticut shore, the mean daily tidal ranges at various stations are: Stonington, 2.7 feet; New London, 2.5 feet; Saybrook, 3.6 feet; New Haven, 6 feet; Greenwich, 7.4 feet. As elsewhere along oceanic coasts, however, the tidal range for any given locality is not constant, but varies from time to time. The most important of these variations are seen in the semi-monthly spring and neap tides. The spring tides, occurring just after the new moon and the full moon each month, have a range from sixteen to twenty per cent greater than the average, and about twice that of the neap tides, which occur just after the first and last quarters of the moon. The equinoctial high tides, which occur at about the time of the equinoxes, rise considerably higher than the spring tides; while storm tides, especially those in which the spring tides are coincident with strong onshore gales, may rise from three to five feet higher than the mean high tide level.*

Illumination at different depths.—In proceeding from high tide mark downward into the depths of the sea there is a gradual

* For a very clear and comprehensive account of the tides and their making, see Wheeler ('06).

decrease in the amount of illumination received by plants growing on the bottom, and the intensity (or the quality) of the light at different depths is one of the most important factors controlling the distribution of many seaweeds. Taken collectively, the seaweeds of the four great natural groups of algae (the blue-greens, the greens, the browns, and the reds) differ considerably from one another in their light requirements. The blue-green and the green algae demand the greatest illumination and the red algae the least, while the brown algae are intermediate in their light requirements. The blue-greens and greens are most abundant in areas which are above low tide level; toward high tide mark they are practically the only forms present. The browns, in large part, flourish best in the regions just above and just below low tide level. The reds are most luxuriantly developed below low tide mark; in deep water they are the commonest forms. To be sure, there are numerous exceptions; certain of the red algae, under favorable conditions, range well up toward high tide mark*; certain of the green algae grow in deep water; while along our coast certain of the brown algae, viz. the kelps, are the most conspicuous members of the algal vegetation in the deeper waters. Generally speaking, however, the vertical distribution of marine algae along the coast, at least below low tide level, is closely correlated with variations in light.†

The extreme depths at which autophytic marine algae will grow depends largely on the clearness of the water. Some species have been collected, in very clear water, at depths of more than

* It is of interest, in this connection, to note that *Chondrus crispus*, one of the most characteristic of the red algae along the Connecticut coast and a species which ranges from deep water up to low tide level, frequently loses its red color completely when growing near the surface, becoming yellowish green.

† But whether it is the quantity of the light or its quality that determines the depth at which various algae will grow is a matter of dispute. To quote from B. M. Davis ('13), "The red rays of sunlight, it is claimed, cannot penetrate much below 7 fathoms, and the light at greater depths is mainly composed of blue and green rays, is feeble in yellow, and lacks red rays entirely. Certain investigators . . . hold that the quality of the light rather than its intensity determines the distribution of the green, brown, and red algae. According to this view the green algae grow under bright illumination because they require the maximum of red rays, while the red algae are able to live in deeper water because their color allows them to absorb the green rays which they especially need. The brown algae in general adjust themselves to light conditions intermediate between these extremes."

400 feet. B. M. Davis ('13) mentions twelve red algae and two browns which, in the vicinity of Woods Hole, Massachusetts, have been found growing in water from 100 to 115 feet in depth. No data are available for Long Island Sound.

Temperature of sea water.—Differences also in the temperature of the water unquestionably play an important part in determining the distribution of various marine algae, especially of forms that grow below low tide level, and the character of various associations of seaweeds may thereby be influenced to a marked degree. Thus, the dissimilarities between the algal vegetation of sheltered waters and that of more exposed waters seem to be associated in large measure with differences in temperature. Sheltered waters are warmer in summer and may be colder in winter than are exposed waters; they exhibit a much higher range of temperatures from season to season. B. M. Davis regards the temperature factor as of such fundamental significance that in classifying the sublittoral associations of the Woods Hole region he divides them primarily into two groups: the cool water sublittoral formation and the warm water sublittoral formation. The former embraces the associations of areas in which the temperature at the bottom is relatively cool during the summer months, particularly of situations which are exposed to the open sea. The latter embraces the associations of areas in which the temperature at the bottom is relatively warm during the summer months, particularly of situations which are sheltered from the open sea. Many of the seaweeds which are found only during winter and spring in the more sheltered situations flourish throughout the year in more exposed waters. The influence of differences in the temperature of the water is further seen in the pronounced seasonal periodicity exhibited by many algae. Thus, some species which are very conspicuous during winter and spring seem to disappear completely during the summer, while others, which are prominent in summer, are apparently absent in winter.

B. PHYSIOGRAPHIC INFLUENCES

Erosion and deposition.—Nowhere is the influence of erosion and deposition on the character of the vegetation more apparent than along the seacoast. Here, as elsewhere, dynamic forces of

the geologic past are in part responsible for the larger features in the landscape, but even more important in their influence are the physiographic agencies of today. The wearing away of the shore here, and its building up there, the development in exposed situations of coastal swamps, beaches and dunes—these and similar phenomena are due primarily to the activity of waves, of tidal and other currents, and, in the case of the dunes, of wind. Erosion and deposition, therefore, have an important influence on the plant associations, since the character of seaside vegetation, both above and below high tide level, bears an intimate relation to the physical nature of the substratum. Thus, the plant associations of sandy shores differ markedly from those of muddy shores, and, again, from those of rocky shores. Seaweeds, for example, are most luxuriantly developed on rocky or stony bottoms; on sandy or muddy bottoms they may be almost absent; and so on.*

Other agencies.—The influence of ice and of salt spray are further factors which may contribute materially to the character of plant associations along the seacoast. Floating ice, in addition to the indirect effect which it may exert by supplementing the abrading action of the waves, scrapes exposed rocks bare of seaweeds and in other ways affects the shore vegetation within its reach. Salt spray dashed up by waves or wind sometimes makes possible the existence of certain marine algae even above high tide mark, at the same time preventing the development here of non-halophytic land plants or at any rate having a more or less pronounced effect on their growth. The sterility in mineral nutrients of wave- and wind-deposited sand is very likely responsible, in part at least, for the peculiarities of beach and dune vegetation.

C. ATMOSPHERIC INFLUENCES

Various atmospheric agencies which tend to accelerate transpiration, especially strong winds and, during certain seasons of the year, intense heat, may affect to a marked degree the habit and structure of terrestrial plants along the seacoast. Strong illumination, likewise, may be an influential factor. The effect

* For purposes of convenience, throughout the present paper and the next one a distinction is made between *shore* and *bottom*. The application of the term shore is restricted to areas above low tide level, areas below low tide level being referred to as bottom.

of these influences is seen, for example, in the markedly xerophytic nature of the vegetation on sandy beaches and dunes; it is further reflected in the relatively xerophytic nature of the algal vegetation of the intertidal region, as compared with that of areas which are continuously submerged.

III. CLASSIFICATION OF PLANT ASSOCIATIONS ALONG THE SEACOAST

Introductory.—In a general way, the various factors which determine the distribution of plant associations along the seacoast can be summed up under two heads: (*a*) factors associated with differences in physiography, and (*b*) factors associated with differences in tide level. The physiographic influences, in the

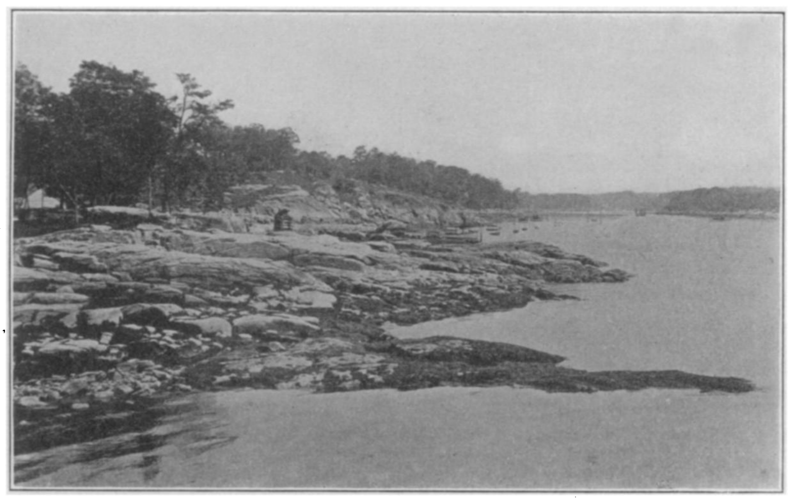

FIG. 1. Rocky shores of the eroding type; East Haven. View, taken at about low tide, shows rockweed vegetation in lower foreground.

main, can perhaps best be grouped under two heads: erosion and deposition. Areas along the coast where the influence of currents and waves is such that erosion predominates are termed *eroding areas*. Areas where deposition predominates are termed *depositing areas*. Along an irregular coastline, such as that of southern Connecticut, eroding and depositing areas may alternate with one another in rapid sequence, erosion tending to predominate wherever there are salients in the shore-line, deposition wherever

there are reëntrants. The more important influences associated with the presence of salt water may be grouped under the head of tide levels. Roughly speaking, it can be said that the distribution in a horizontal direction of the various seaside types of plant association is determined largely by their physiographic relations,* their distribution in a vertical direction largely by their relation to tide levels. In classifying these associations, then, both sets of relations must be taken into consideration.

Plant associations grouped in relation to physiography.—With reference to their physiographic relations the plant associations

FIG. 2. Depositing shores near Watch Hill, Rhode Island; essentially similar to corresponding areas in Connecticut. Beach and line of dunes (with *Ammophila*) to right and in foreground; salt marshes in left mid-distance.

along the seacoast may be divided into two groups: *the associations of eroding shores and bottoms*, and the *associations of depositing shores and bottoms*. The essential features of an eroding shore (FIGS. 1, 3, etc.) are the presence of bluffs and headlands and the absence or sparse development of beaches, dunes and marshes. Depositing shores (FIG. 2), on the other hand, are characterized by the presence of beaches, dunes and marshes, and by the ab-

* This generalization applies strictly only along the shores of the open Sound, since of course differences in the salinity of the water also affect the horizontal distribution of the plant associations where the salty waters of the sea meet the fresh waters of inflowing streams.

sence of bluffs and headlands. Eroding bottoms, as a rule, are rocky, stony, or shelly; depositing bottoms are muddy or sandy. So significant are these physiographic differences that in the detailed account which follows the plant associations have been grouped primarily with reference to their physiographic relations, their relation to tide levels being used as a secondary means of subdivision.

Plant associations grouped in relation to tide levels.—With reference to the relation of the substratum to tide levels, three regions may be distinguished: the *littoral*, the *sublittoral*, and the *supralittoral*. The limits of these regions have been variously described by different writers;* as used in the present treatment they may be defined as follows. The littoral region comprises that part of the shore which lies between mean low tide level and mean high tide level. The sublittoral region extends from mean low tide level (the lower limit of the littoral) downward and seaward as far as the maximum depth at which the higher algae grow. The supralittoral region extends from mean high tide level (the upper limit of the littoral) upward and landward as far as the character of the vegetation is definitely associated with the proximity of the sea.

Corresponding approximately with these regions, the plant associations of the seacoast can be divided into three groups. The littoral region is characterized by associations of plants which are adapted to endure alternate daily submergence by tidal waters and exposure to the air; the sublittoral region by associations of plants which are adapted to endure continuous submergence; and the supralittoral region by associations of plants which are

* By derivation, the term *littoral* (used both as a noun and as an adjective) means simply "of or pertaining to the seashore," and in this sense the word has often been used more or less indiscriminately with reference to plants or plant associations occurring anywhere along the seashore. Technically, and particularly in ecologica literature, this term has come to be used somewhat more strictly, but, even so, its application in practise has been far from uniform. Three recent writers, for example, have used it in as many different ways. Johnson and York ('15) define the littoral in the sense in which it is used in the present paper; B. M. Davis ('13) describes it as "the zone extending from low water mark to the highest point at which marine algae cease to grow;" while Transeau ('13) seems to embrace in the littoral all areas, both below and above low tide level, which are "occupied by the shore drift in transit." The terms sublittoral and supralittoral likewise are capable of various interpretations (see discussions by Sumner, Osburn and Cole, '13, B. M. Davis, '13, and Johnson and York, '15).

adapted to endure continuous exposure to the air. The characteristic plants of the supralittoral region are terrestrial seed plants; those of the sublittoral are marine algae, together with a few aquatic seed plants; while the plants of the littoral include both seed plants of terrestrial derivation and algae of marine derivation. But while, broadly speaking, these three groups of plant associations are very distinct from one another, it is rarely possible to draw sharp lines of demarcation between them. The principal reason for this is obvious, namely, the recurrent fluctuations in the height of the tides. Thus, in the upper levels of the sublittoral region there is an area which ordinarily is submerged at low tide, but which is uncovered by the semi-monthly spring low tides; and the vegetation here naturally includes elements which are more characteristic of the littoral region above than of the sublittoral. Similarly, in the lower levels of the supralittoral region there is an area, ordinarily exposed, but flooded by the spring tides, in which the vegetation may differ quite markedly from that of areas which are never submerged. The equinoctial tides, storm tides, and wave-dashed spray likewise may exert a modifying effect on the character of the associations in the supralittoral.

In some ways it might seem desirable to group the plant associations of the seacoast primarily with reference to tide levels, treating their physiographic relations as of secondary importance. Such a grouping, however, would not be in harmony with the larger physiographic scheme of classification which embraces, not alone the associations of the seacoast, but all other types of vegetation in Connecticut as well.*

IV. THE VEGETATION OF ERODING AREAS AND ITS ECOLOGICAL RELATIONS

A. ROCKY SHORES AND BOTTOMS†

1. Seaweed associations of the sublittoral region

Introductory.—The sublittoral region can be divided into two fairly well-defined "sub-regions": the *upper sublittoral* and the

* This is essentially the scheme used by Transeau ('13) and by Johnson and York ('15).

† With reference to the physical character of the surface acted upon by the waves, two general types of eroding shore can be distinguished along the Connecticut coast:

lower sublittoral. The former includes the bottom between low tide mark and a depth of from four to six feet; the latter includes all of the sublittoral below this depth. The vegetation of both these zones, on rocky, stony or shelly bottoms, consists wholly of marine algae, except as there may be an occasional sparse growth of eel grass. Essentially all of the seaweeds to be mentioned in the lists which follow are attached forms: in large part they find a foothold on rocks, stones, or shells; but many of them, particularly among the smaller species, also grow as epiphytes on other seaweeds, or on eel grass. No account whatever is taken here of the vast assemblage of microscopic free-floating algae which constitute what is known as the plankton, nor of the various attached forms included among the diatoms. In the discussion of the seaweed associations which follows, the published works of Hall ('76), Farlow ('79), Collins ('00, '05), B. M. Davis ('13), Transeau ('13), and Johnson and York ('15) have been freely drawn upon, and the lists of species have been checked over by Mr. F. S. Collins, whose published lists of marine algae (*op. cit.*) have been followed in matters of algal nomenclature.

Associations of the lower sublittoral.—By far the greater number of seaweeds characteristic of the lower sublittoral region belong to the red algae, while the green algae are practically absent here. The brown algae are represented by comparatively few species, but among these are the kelps, particularly *Laminaria Agardhii*, which are conspicuous by their large size, individual plants often acquiring a length, along our shores, of ten or more feet. Little of a definite nature can be stated with regard to the grouping into associations of the algae in the lower sublittoral, and many of them are seldom seen, except as washed ashore during storms. Some of the larger species, however, frequently form extensive beds.* Most of the species characteristic of the lower sublittoral

(*a*) *eroding rock shores*, where the substratum consists of firmly compacted rock, *i.e.*, of rock in the ordinarily accepted sense; and (*b*) *eroding drift shores*, where the substratum consists of glacial drift, which technically may be classed as uncompacted rock. The general description which follows applies more particularly to rock shores and bottoms, but attention will be directed later to resemblances and differences between the vegetation here and that along eroding drift shores.

* Regarding the associational relations of the algae of the littoral and sublittoral regions in the vicinity of Woods Hole, B. M. Davis ('13) remarks that "groups of species may cover large areas and even form broad zones of vegetation . . . but

grow best in strongly saline waters bordering the open ocean, and in Long Island Sound they develop much more luxuriantly eastward, toward the entrance, than westward, toward the head of the Sound. In general, there is little question that the algal vegetation of the lower sublittoral is much more poorly developed along the Connecticut shore than, for example, in the Woods Hole region. A list of species characteristic of the lower sublittoral in this region is given below, but while all of these are known to be more or less abundant in Long Island Sound, sufficient data are not available to permit generalizations regarding their relative frequency.*

BROWN ALGAE (*Phaeophyceae*)

Chorda Filum	CW	*Laminaria Agardhii*	CW
Cladostephus verticillatus	CW	*Laminaria digitata*	C
Desmarestia aculeata	CW	*Sargassum Filipendula*	W
Desmarestia viridis	CW		

RED ALGAE (*Rhodophyceae*)

Agardhiella tenera	CW	*Hildenbrandtia Prototypus*	CW
Ahnfeldtia plicata	CW	*Lomentaria uncinata*	W
Antithamnion cruciatum	CWZ	*Phyllophora Brodiaei*	CW
Ceramium rubrum	CWZ	*Phyllophora membranifolia*	CW
Ceramium strictum	WZ	*Plumaria elegans*	C
Ceramium tenuissimum	WZ	*Polyides rotundus*	CW
Champia parvula	W	*Polysiphonia elongata*	CW
Chondrus crispus	CW	*Polysiphonia nigrescens*	CW
Corallina officinalis	CW	*Rhodymenia palmata*	CW
Cystoclonium purpurascens	CW	*Rhodomela Rochei*	CW
Dasya elegans	WZ	*Seirospora Griffithsiana*	WZ
Delesseria sinuosa	C	*Spermothamnion Turneri*	CW
Griffithsia Bornetiana	W	*Spyridia filamentosa*	WZ
Grinnellia americana	CW		

Associations of the upper sublittoral.—Many seaweeds of the lower sublittoral commonly range upward to low tide level. The so-called Irish moss (*Chondrus crispus*), for example, a flat-fronded, purplish red species with pronounced dichotomous

the vegetation more often consists of small and more scattered groups, the limits of which are generally more easily recognized and in which a single species usually predominates." These groups he terms associations. For the Woods Hole region he distinguishes nearly sixty such associations or groups of associations.

* The letters C and W, placed after various species in this and the following list, are taken from B. M. Davis ('13). They indicate respectively species which, in the Woods Hole region, he includes in the cool-water or in the warm-water sublittoral formation. The letter Z indicates species which he includes in the *Zostera* formation, to be treated by the writer in the paper which will follow this one.

branching, which sometimes grows in water more than a hundred feet deep (in the Woods Hole region) and which is a characteristic component of the lower sublittoral flora, probably nowhere develops more luxuriantly than in the upper sublittoral, where it commonly occurs in great profusion on exposed rocks just below low tide mark. Another form which is prominent in this zone, as well as in the lower sublittoral, is *Ceramium rubrum*, a profusely branched, bright red, filamentous species. This plant probably has a more ubiquitous distribution along the Connecticut coast than any other red alga. Still another red of the lower levels which thrives in the upper sublittoral is *Hildenbrandtia Prototypus*, a species which forms conspicuous reddish incrustations over rock surfaces. In fact, there are probably few algae of the deeper waters which, under favorable conditions, do not range upward to low tide level at certain seasons of the year, and some of them, e.g., *Ceramium* and *Hildenbrandtia*, may extend upward locally well into the littoral region.

But the outstanding feature of the vegetation in the upper sublittoral is the presence of certain seaweeds which do not occur in deep water, or which develop most prolifically near the surface. Especially characteristic are certain green algae, viz., *Bryopsis plumosa* and various species of *Cladophora*; certain browns, e.g., *Ectocarpus* spp., *Pylaiella littoralis*, and *Phyllitis fascia*; and certain reds, e.g., *Nemalion multifidum* and various species of *Callithamnion* and *Polysiphonia*. Indeed, it seems not unlikely that the scarcity near the surface of many of the red algae of deeper waters is due in large measure to their inability to compete successfully with these other species which thrive so luxuriantly in this region. Taken as a whole, the plant population of the upper sublittoral comprises an intimate admixture of green, brown, and red algae, but with the reds numerically the strongest. Locally and at different seasons of the year various associations and groups of associations can be distinguished, and, in particular, various of the species already mentioned as characteristic of the upper sublittoral commonly form conspicuous masses of vegetation. A list of algae characteristic of the upper sublittoral in Long Island Sound is given below. Some of these are restricted to these upper levels, particularly among the greens and browns; but

many, among them most of the reds, range to much greater depths.

GREEN ALGAE (*Chlorophyceae*)

Bryopsis plumosa	W	*Cladophora gracilis*	CWZ
Chaetomorpha Linum	CW	*Cladophora lanosa*	W
Cladophora albida refracta	CW	*Cladophora rupestris*	CW
Cladophora arcta	W	*Ulva Lactuca*	

BROWN ALGAE (*Phaeophyceae*)

Castagnea virescens	WZ	*Phyllitis fascia*	
Chorda Filum	CW	*Punctaria latifolia*	
Chordaria flagelliformis	CW	*Pylaiella littoralis*	W
Ectocarpus confervoides	CWZ	*Ralfsia clavata*	CW
Ectocarpus siliculosus	CWZ	*Sargassum Filipendula*	W
Leathesia difformis	CW	*Scytosiphon lomentarius*	
Mesogloia divaricata	W	*Sphacelaria cirrhosa*	W

RED ALGAE (*Rhodophyceae*)

Antithamnion americanum	W	*Gracilaria multipartita*	W
Callithamnion Baileyi	WZ	*Grinnellia americana*	CW
Callithamnion roseum	WZ	*Hildenbrandtia Prototypus*	CW
Callithamnion tetragonum	W	*Lomentaria uncinata*	W
Ceramium rubrum	CWZ	*Melobesia pustulata*	CW
Ceramium strictum	WZ	*Nemalion multifidum*	
Champia parvula	W	*Polysiphonia fastigiata*	W
Chondria dasyphylla	WZ	*Polysiphonia fibrillosa*	W
Chondria tenuissima	W	*Polysiphonia urceolata*	C
Chondrus crispus	CW	*Polysiphonia variegata*	W
Corallina officinalis	CW	*Polysiphonia violacea*	CW

2. Seaweed associations of the littoral region

Introductory.—The vegetation of the littoral along eroding rocky shores, like that of the sublittoral, is composed of seaweeds; but the ecological relations of the seaweeds growing in these two regions are very dissimilar.* In comparison with the strictly hydrophytic species of the sublittoral, the characteristic seaweeds of the littoral are relatively xerophytic. As in the case of the sublittoral region, however, the vegetation of the littoral is by no means uniform throughout and, with reference primarily to vegetational dissimularities, this region likewise can be divided into two "sub-regions": the *lower littoral* and the *upper littoral*.†

* See earlier discussion of these relations, pp. 99, 100.

† Along depositing muddy shores, as will be seen later, sharply defined differences in the character of the vegetation at different levels clearly differentiate the area here termed the lower littoral into two parts, designated by Johnson and York

The boundary between these two subdivisions lies approximately at the average level of neap high tides, or a little below, but it varies locally and, in favorable situations, the vegetation of the lower littoral may extend well up toward mean high tide mark.

Associations of the lower littoral.—The characteristic plants of the lower littoral along eroding shores are the rockweeds, *Ascophyllum* and *Fucus* (FIGS. 3 and 4). These conspicuous olive-brown seaweeds grow in massive profusion and commonly plaster

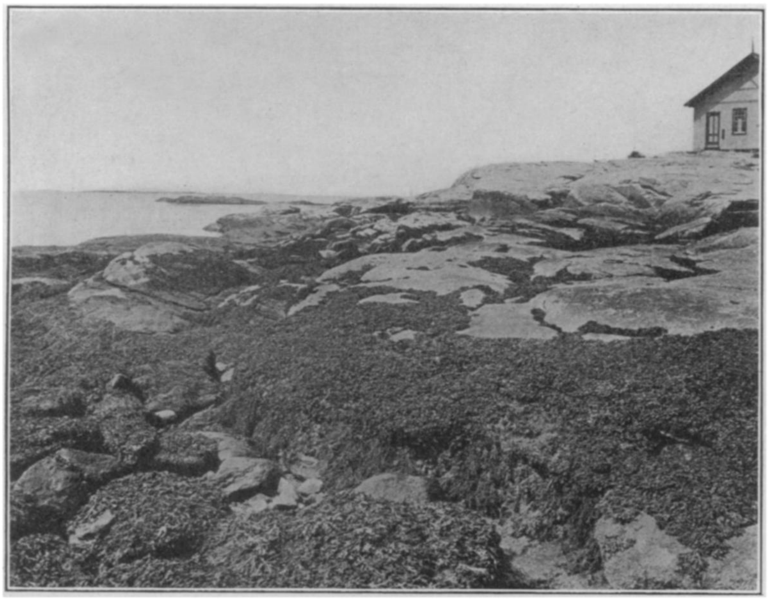

FIG. 3. Granitic eroding shore at low tide, showing dense growth of *Ascophyllum* and *Fucus* in the littoral region; East Haven.

over almost completely with their coarse, leathery, forked fronds the surfaces of rocks, occurring also, though perhaps less luxuriantly, on piles and other woodwork. The two may grow intermixed, or one or the other may predominate locally. *Fucus* usually ranges somewhat nearer high tide mark than *Ascophyllum*, and along rocky shores the upper limit of the lower littoral may be regarded as coinciding approximately with the upward limit of

('15) the *lower littoral* and the *midlittoral*. A similar subdivision can be made along other types of shore (as Johnson and York have done), but the vegetational dissimilarities here are much less apparent and for this reason the writer has chosen, excepting along depositing muddy shores, to include in the lower littoral all of the mean intertidal region below the upper littoral.

range for this plant. Locally, however, the rockweeds are scarce or absent, and it is mostly in areas of this description, or as epiphytes on the rockweeds, that the various other algae listed below occur. *Chaetomorpha*, *Rhizoclonium*, and *Scytosiphon*, however, commonly grow in tidal pools. The following seaweeds may be regarded as characteristic of the lower littoral.

GREEN ALGAE (*Chlorophyceae*)

Bryopsis plumosa	*Enteromorpha intestinalis*
Chaetomorpha spp.	*Rhizoclonium* spp.
Enteromorpha clathrata	*Ulva Lactuca*

BROWN ALGAE (*Phaeophyceae*)

Ascophyllum nodosum	*Phyllitis fascia*
Ectocarpus spp.	*Pylaiella littoralis*
Fucus platycarpus	*Ralfsia clavata*
Fucus vesiculosus	*Scytosiphon lomentarius*

RED ALGAE (*Rhodophyceae*)

Ceramium rubrum	*Nemalion multifidum*
Ceramium strictum	*Polysiphonia fastigiata*
Hildenbrandtia Prototypus	*Porphyra laciniata*

Some of these species, it will be noted, are also characteristic of the upper sublittoral, and in deep tidal pools still others of these sublittoral algae may be represented, but it is seldom that any of them range far above low tide mark.* Aside from the rockweeds, perhaps the most conspicuous algae of the lower littoral are *Phyllitis* and *Porphyra*, although the sea lettuce, *Ulva Lactuca*, is sometimes prominent.

Associations of the upper littoral.—The chief factor in limiting the upward extension of the rockweeds and other seaweeds that are found in the lower littoral, but not in the upper, is dessication. Along perpendicular sea walls which are protected from intense illumination these plants reach higher levels than along shores where they are exposed to strong sunlight. The drying effect of air and sun throughout much of the upper littoral is commonly so great that between tides the seaweeds growing here become to all appearances completely dried out and frequently the more delicate forms become baked tight to the rock surface. Very few marine

* Locally, almost any of the species here listed as characteristic of the lower littoral may range downward below mean low tide mark. This is true, for example, of both *Ascophyllum* and *Fucus*.

algae can endure such extreme conditions and largely for this reason the algal vegetation at the higher levels is very much impoverished: in fact, along many rocky shores there is practically no vegetation toward high tide mark. The red algae are frequently represented in the upper littoral by the relatively xerophytic *Bangia fusco-purpurea*; but the browns, except for species that may inhabit tidal pools or which may occasionally push their way up from the lower littoral, are absent. The characteristic algae of this zone are certain greens, particularly, species of *Enteromorpha* (FIG. 4). The two species of this genus listed for

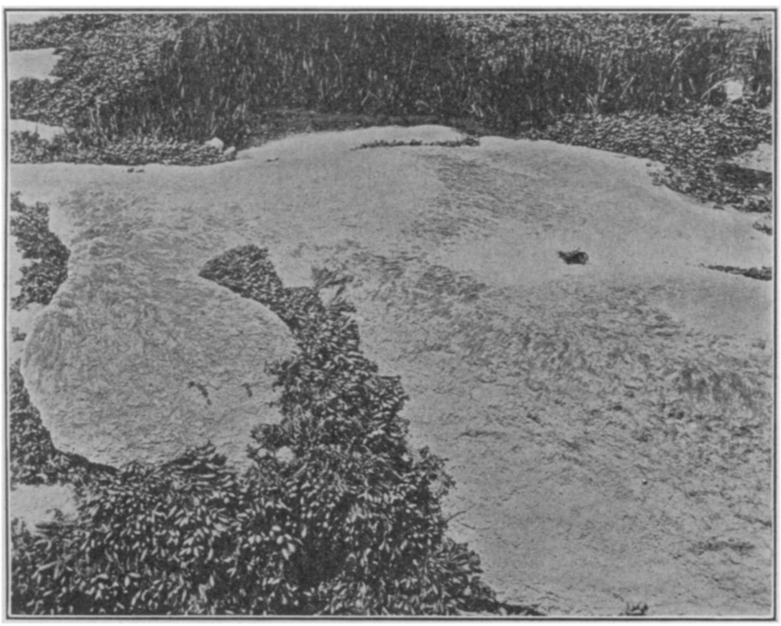

FIG. 4. *Fucus* and *Enteromorpha* on granitic shore; East Haven. The *Enteromorpha* appears as a dark streaking on the otherwise bare rock surface.

the lower littoral (*E. clathrata* and *E. intestinalis*) may occur in the upper littoral as well, but there are two other species of this genus, viz., *E. minima* and *E. prolifera*, which apparently are restricted to this region. In addition to the enteromorphas, the following algae frequently are represented more or less abundantly in the upper littoral: (greens) *Urospora penicilliformis*, *Rhizoclonium* spp., *Ulothrix* spp.; (blue-greens) *Calothrix* spp.

3. Associations of the supralittoral region

The associations of rocky sea bluffs.—Like the sublittoral and the littoral regions, the supralittoral (FIG. 5) can be divided into a lower and an upper "sub-region." The *lower supralittoral* comprises a belt immediately above mean high tide mark in which, except frequently for an impoverished growth of *Enteromorpha* spp., the rock surface is practically destitute of vegetation of any description. Conditions here are too dry for seaweeds and too salty for lichens and mosses, while the development of halo-

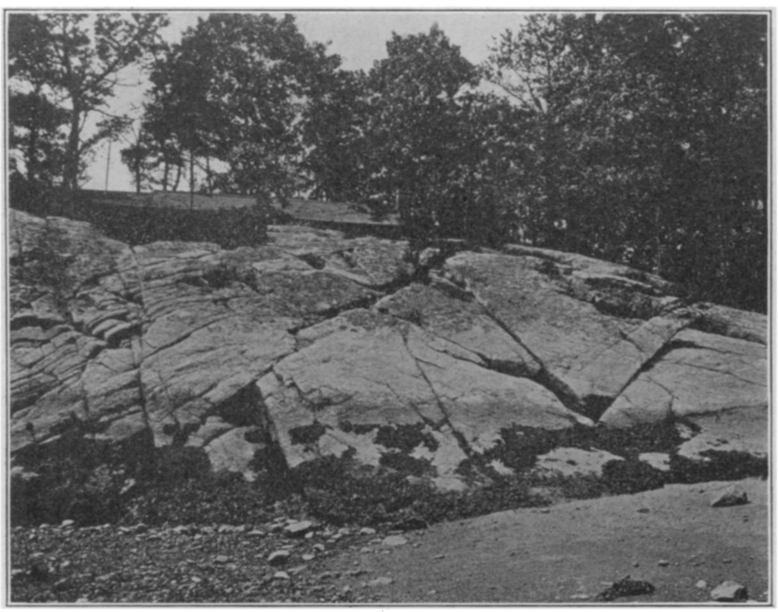

FIG. 5. Zonation of plant associations along a rock-bound shore; East Haven. The following zones are apparent, from below upward: (1) *Fucus* and *Ascophyllum* of lower littoral; (2) *Enteromorpha*, etc., of upper littoral; (3) plantless lower supralittoral; (4) lichen-moss zone of upper supralittoral, with seed plants above.

phytic seed plants is prevented primarily by the mechanical action of waves and ice in times of heavy sea. This plantless belt varies in width: along the more exposed shores it may extend upward for a distance of twelve or fifteen feet; in less exposed situations it may be quite narrow.

The *upper supralittoral* extends from the upper edge of the

lower supralittoral upward and away from the water to where the influence of the sea virtually ceases. The vegetation here consists, primarily, of various rock-face and crevice lichens. Sometimes there is a more or less distinct lichen-moss zone just above the plantless region, but, as a rule, the crevices at any rate support, even here, a limited assortment of vascular plants. Prominent among these latter, especially in the more exposed situations, are various more or less halophytic species: such, for example, as *Carex silicea, Juncus Gerardi, Lathyrus maritimus, Prunus maritima, Plantago decipiens,* and *Solidago sempervirens.* Other characteristic plants of the upper supralittoral along rocky shores are listed below.

Juniperus virginiana	*Pyrus arbutifolia atropurpurea*
Deschampsia flexuosa	*Amelanchier* sp.
Danthonia spicata	*Rosa humilis*
Poa compressa	*Rhus typhina*
Poa pratensis	*Rhus Toxicodendron*
Festuca rubra	*Psedera quinquefolia*
Festuca octoflora	*Hypericum gentianoides*
Smilacina stellata	*Opuntia vulgaris*
Smilax glauca	*Gaylussacia baccata*
Myrica carolinensis	*Anagallis arvensis*
Rumex Acetosella	*Achillea Millefolium*
Sagina procumbens	*Chrysanthemum Leucanthemum*

It will be noted that, except for *Sagina,* all of the plants here mentioned are xerophytic, light-requiring species. Indeed, aside from the presence of the halophytic element, the associations of the upper supralittoral along the seacoast differ but little from the pioneer associations elsewhere developed on ordinary rocky uplands. Toward the upper edge of the supralittoral region there commonly occurs a dense thicket of bayberry, sumac, poison ivy, and various others of the shrubs and vines listed.

B. SHORES AND BOTTOMS OF GLACIAL DRIFT

1. Associations of the sublittoral region

The associations of stony bottoms.—Where the substratum acted on by the forces of erosion is glacial drift, most of the finer detritus commonly is carried away by the currents, leaving behind on the bottom the boulders formerly present in the drift but too heavy to be transported. This type of bottom is a common one along exposed parts of the Connecticut shore line, yet little need be

said regarding its vegetation, since it is essentially similar to that of rocky bottoms. As a rule, the boulders are more or less scattered, and between them, in areas protected from erosion by the boulders themselves, the bottom is sandy. The vegetation in such places resembles that of depositing sandy bottoms, to be described in a later paper.

2. Associations of the littoral and supralittoral regions

Eroding shores of glacial drift compared with rocky shores as an environment for plants.—Even along a rock-bound coast the influence of waves and ice on the character of seaside vegetation is very apparent; but, as compared with the conditions along shores of glacial drift, their influence there is relatively inconsequential. Along rock shores the influence of these physiographic agencies on plants is direct, and it is confined to areas within actual reach of the waves. Along shores of glacial drift their indirect influence may be even more important; for here the undermining and abrading effect of the waves, dashing against the soft, uncompacted rock, not only influences the vegetation within reach but that at higher levels as well. The contrast is quite analogous to that pointed out elsewhere in comparing rock ravines with ravines in glacial drift.*

Associations of the supralittoral.—Wherever deposits of glacial drift are exposed to wave action, the natural result of the washing away of the soil on vegetation is the partial or complete destruction of whatever plant associations may happen to have been present. Associations along the entire face of an eroding bluff may thus become completely annihilated, so that, in extreme cases, the bluff will be virtually barren of vegetation of any description. But, as a rule, plants are not entirely absent here. For the forces of erosion are most active during winter and early spring, which is a period of inactivity for plants; during the growing season there is practical freedom from erosion. In consequence, even an actively eroding bluff may support a scattered population of plants, mostly annual species which are able to mature between successive periods of erosion; and, on bluffs

* See Nichols, '16, p. 237, etc. Also, in this connection, compare Cowles's description of the conditions on eroding clay bluffs along Lake Michigan (Cowles, '01, p. 50 et seq.).

where the periods of erosion are separated by periods of years, perennial herbs and shrubs may become established.

The vegetation of eroding bluffs in glacial drift usually includes, in varying abundance, various of the herbaceous xerophytes elsewhere listed as characteristic of rock bluffs (see list on p. 109), together, commonly, with such additional species as *Equisetum arvense*, *Polygonum scandens*, *Oenothera muricata*, *Apocynum cannabinum*, *Verbascum Thapsus*, *Ambrosia artemisiifolia*, and *Solidago lanceolata*. It may also include, especially below, such distinctively seaside plants as *Lathyrus maritimus*, *Cakile edentula*, and *Solidago sempervirens*. In addition to this, in the main, essentially pioneer flora there usually are present various relicts of the preexisting vegetation, especially plants which formerly grew toward the top of the bluff and have survived on raft-like clumps of earth that have slid down the slope (i.e., "*slump plants*").

In the lower supralittoral, between ordinary high tide level and the base of an eroding bluff, as a rule, there is a narrow fringe of stony, gravelly, or sandy beach. The vegetation here resembles that of the corresponding region on shingle and sandy beaches, to be described later.

Associations of the littoral.—Along the base of an eroding bluff of glacial drift, the littoral region ordinarily is occupied by a rather steep, stony beach, built up out of boulders and stones of all sizes which have been washed out of the bluff itself. The vegetation here, though ordinarily less well developed (as in the area illustrated by FIG. 6), is essentially similar to that of the littoral along rocky coasts, except that frequently there is an incursion of associations characteristic of depositing shores, favored by the protection from wave activity which the boulders afford. Thus, it is not unusual here to find incipient salt marshes developed here, in among the boulders of the littoral (FIG. 6).

C. FOREST GROWTH ON UPLANDS ADJOINING THE SHORE

Along the relatively sheltered Connecticut coast the vegetation of sea bluffs and headlands is much less distinctive than along very exposed coasts, such as that of northern Cape Breton (see Nichols, '18, p. 319 et seq.), and the influence of the sea on the character of

the forests and forest trees near the shore is much less marked. It is only occasionally here that trees are encountered which exhibit the weather-beaten, one-sided aspect so familiar along more exposed coasts, and the forests immediately adjoining the shore may differ but little from forests developed in similar situations inland. There is a general tendency, however, for these forests to

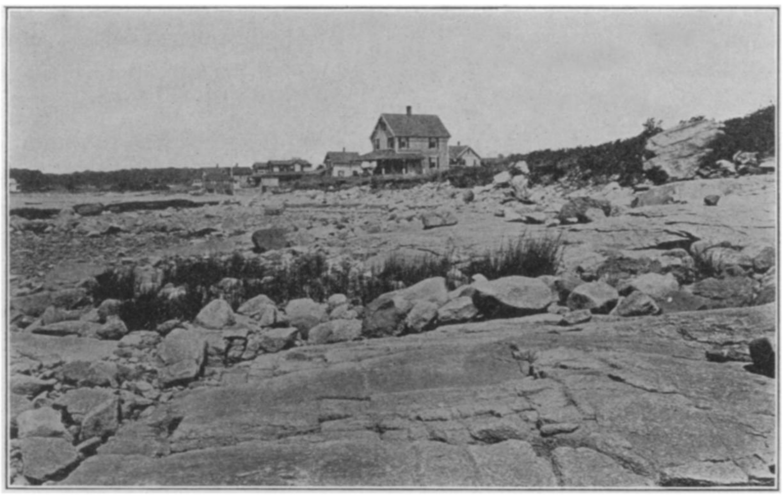

FIG. 6. Eroding shore with stones and boulders derived from glacial drift (seen above) which formerly covered entire area; East Haven. Miniature salt marsh in foıeground; also, in foreground, outcrop of granite exposed by removal of drift.

be relatively open and somewhat xerophytic. On many of the small rocky islands which occur scattered along parts of our coast, for example, the forest is made up largely of pitch pine (*Pinus rigida*), and the bulk of the undergrowth consists of the shrubs which have been listed as characteristic of the upper supralittoral along rocky shores (see p. 109). On some of these islands an appreciable difference can be observed between the forest growth of windward and lee slopes (assuming the effective winds to blow from off the sea). On one of the larger and more primitive of the Thimble Islands, for example, the prevailing type of vegetation is an open forest, predominantly pitch pine, but with a scattering of hickory (*Carya* spp.), black oak (*Quercus velutina*), sassafras (*Sassafras variifolium*) and red maple (*Acer rubrum*), and with the undergrowth as described above. On lee slopes,

however, the forest is less open; beech (*Fagus grandifolia*), basswood (*Tilia americana*), red oak (*Quercus rubra*), and chestnut (*Castanea dentata*) are common; and the undergrowth includes witch hazel (*Hamamelis virginiana*) and mountain laurel (*Kalmia latifolia*), elsewhere absent.

D. SUCCESSIONAL RELATIONS ALONG ERODING COASTS

Successional changes in the character of plant associations along the seacoast result primarily from changes in physiography, and where the physiography is essentially stable for long periods of time the vegetation likewise, except for seasonal variations, may remain practically unchanged. Thus, along an eroding rocky coast, the arrangement of the seaweed associations into definite zones in relation to tide levels has no successional significance: this arrangement, of itself, is scarcely less permanent than are the tides. In the upper supralittoral along the coast, as on rocky uplands elsewhere, there is an undoubted tendency for the vegetation to become more mesophytic, but the extent to which any such changes can actually take place is pretty definitely limited by edaphic factors.

Along eroding coasts in glacial drift, however, the conditions are quite different from those along rocky coasts. Here, owing to the unstable nature of the substrata acted on by the waves, changes in topography may be brought about with comparative rapidity. The catastrophic influence of such changes on the preexisting vegetation, elsewhere described (p. 110), may be looked upon as in the nature of a retrogressive succession. Once established, the pioneer vegetation of an eroding bluff may maintain virtually the same aspect year after year, or just as long as the bluff continues to be acted on, at more or less frequent and regular intervals, by the agencies of degradation. But should erosion cease, due to the accumulation of boulders along the base of the bluff or to the formation of some other protective barrier, then the universal tendency of vegetation everywhere to approach the mesophytic condition becomes at once apparent. A bluff, formerly populated by a scattered assemblage of weeds and other herbaceous xerophytes, may thus become covered with a grassy turf or with a dense thicket of bayberry, sumacs, poison ivy and the like. In many

cases, so favorable are the soil moisture relations along sea bluffs of glacial drift that the vegetation of slopes protected from wave action includes such more or less hydrophytic forms as *Salix cordata*, *Alnus rugosa*, *Rosa carolina*, *Heracleum lanatum*, *Verbena hastata*, and *Sambucus canadensis*.

There is one other phase of succession along the seacoast that may well be suggested here. The courses of the currents, which in large measure determine the nature of the bottom in different areas and, *ipso facto*, the nature of the vegetation growing on the bottom, are by no means constant in their direction and influence. For example, through the development of a sand spit, a strong tidal current may become deflected into an entirely new channel, thereby subjecting what formerly were depositing areas to erosion, and vice versa. Similarly, the development of an off-shore barrier beach may result in an eroding shore becoming transformed into a depositing shore. The importance of such changes in relation to vegetation is self-evident.

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